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A REVISION OF THE GENUS *THERSITES* PFEIFFER (PULMONATA : CAMAENIDAE)

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SUMMARY

Camaenid land snails do share some derived anatomical features and the family should not be characterised in negative terms. The genus name *Thersites* was formerly employed for a large number of Australian camaenids but should be restricted to include only *T. mitchellae* (Cox), *T. novaehollandiae* (Gray) and *T. richmondiana* (Reeve). *Thersites* is characterised by the possession of granular shell sculpture, a dorsal cream coloured line on the neck, a curious bend in the duct of the bursa copulatrix and a large imperforate conical papilla in the penis.

"The appreciation of that indefinable something, which counts for so much in classifying Helices ... this accurate feeling for subtle affinities for which no good reason can be given in words" (Pilsbry 1895: xxii)

INTRODUCTION

The presently accepted classification of the Australian camaenid land snails (Iredale, 1937-38; Burch, 1976) is based almost entirely on shell characters and is largely unworkable. The larger, richly coloured shells of coastal eastern Australia have long been known, but great confusion has always existed, both as to the number of individual species, and to the limits of the genera into which they should be placed. This paper represents the first part of a taxonomic revision of these animals which will attempt to elucidate their phylogenetic relationships and to place their classification on a firmer basis.

FAMILY CAMAENIDAE

Helicoid land snails were originally recognised as a distinct group on the basis of their shell shape and texture. Pilsbry (1895) introduced a new classification of Helices and urged that a natural classification should be based on the consideration of all the organ systems and not upon the shell alone. He divided the "Helicidae" into the subfamilies Polygyrinae, Acavinae, Camaeninae and Helicinae. Apart from the removal of the Acavinae to other places and the upgrading in rank of the taxa, his classification is still recognisable in the most recent compilation by Taylor and Sohl (1962).

The only distinction between the Polygyrinae and the Camaeninae in Pilsbry's diagnosis (1895: xxxii) is that the former were supposed not to possess an epiphallus or flagellum. Later work

(Pilsbry 1940: 575) has shown that this is not always the case. The Camaenidae were characterised thus: genitalia without accessory appendages on the female side; no diverticulum of the duct of the bursa copulatrix; small and numerous eggs; solid smooth or ribbed jaw; radula teeth primitively tricuspid with squarish base plates; shell usually solid, the lip expanded or reflexed. These characters are possessed not only by the Camaenidae but by many other members of the Stylommatophora. We are left with the feeling that certain shell characters, too subtle to express, are the only derived features of the family, and that anatomy has been of little use other than to weed out forms which are clearly not camaenids.

The Camaenidae tended to become a dumping ground for sigmurethran land snails with helicoid shells until Wurtz (1955) pointed out some derived features possessed by the family: the bunches of alveoli in the ovotestis are coalescent; the kidney is primitively at least ten times as long as wide; the kidney is three to four times the length of the pericardium; the left parietal ganglion is fused with the visceral ganglion. Wurtz showed that these features are not shared by the Ammonitellinae (= Megomphicinae) and the Oreohelicinae and that these groups should have separate family status. The Megomphicidae and the Oreohelicidae each have distinct advanced features of their own and cannot be considered as antecedents to the Camaenidae. There is no phylogenetic reason to group the three families in superfamily Camaenacea.

Solem (1973) described the anatomy of the Queensland land snail *Craterodiscus* and assigned it to the "Camaenidae s.l.". In doing so he relied largely upon negative evidence and shared primitive characters, dismissing a large range of sigmurethran taxa as having more advanced character states, before reaching his conclusion. He explained the different pallial configuration as derived from the camaenid state. We do not have information on the jaw and central nervous system, so *Craterodiscus* is only doubtfully a member of the Camaenidae.

Here I am describing a genus which is undoubtedly a member of the Camaenidae for it agrees in all those characters enumerated for the family by both Pilsbry and Wurtz.

GENUS *THERSITES* PFEIFFER (1855)

Type species: *Helix richmondiana* Reeve (1852) by subsequent designation of Martens (1860).

Synonym: *Annakelea* Iredale (1933) new name for *Thersites* with the same type species. When introducing *Annakelea*, Iredale rejected Martens designation stating: "the tautonymic type of *Thersites* must be *H. thersites* Broderip. The latter is not an Australian form at all, so *Thersites* must be dismissed from Australian malacological study". Iredale's view is not upheld and Martens designation is accepted (Zilch 1959-60).

Diagnosis: Eastern Australian camaenid land snails; shell at least 25 mm in width, often keeled, with granular sculpture; there is a light coloured line running between the dorsal grooves on the neck; the seminal receptacle is not extended as a talon beyond the point of entry of the hermaphrodite duct; the duct of the bursa copulatrix has a bend about 1/3 – 1/2 of the way from its junction with the oviduct; the epiphallus bears a flagellum with a pointed tip; a large imperforate conical papilla occupies more than half the length of the cavity of the penis.

History of the genus: Pilsbry (1890: 90) first included only *H. richmondiana* Reeve and *H. novaehollandiae* Gray in *Thersites*, placing the other large eastern Australian camaenids, including *H. mitchellae* Cox, in *Hadra*. He later (1895: 127) considered that *Thersites* and *Hadra* were congeneric and that *Thersites* would have to be used as the genus name for the whole group, in which he recognised *Thersites*, *Xanthomelon* and *Rhagada* as subgenera. Within the subgenus *Thersites* he recognised the sections *Thersites*, *Glyptorhagada*, *Badistes*, *Hadra* and *Sphaerospira*. He assigned *H. mitchellae* to the last of these. Pilsbry received a specimen of *H. mitchellae* from Dr. Cox and discovered that the species possesses a swollen penis containing a large stimulator, and a curious bend in the duct of the bursa copulatrix. This was so much like the condition in *H. richmondiana* figured by his friend Charles Hedley (1889: 62, pl.3) that Pilsbry concluded that *Thersites* and *Sphaerospira* are indistinguishable from the anatomical point of view. In this Pilsbry was wrong, as he did not have the opportunity to examine the type of *Sphaerospira*. *H. fraseri* Griffith and Pidgeon. Had he done so, he would have found that the genital anatomy of *Sphaerospira*

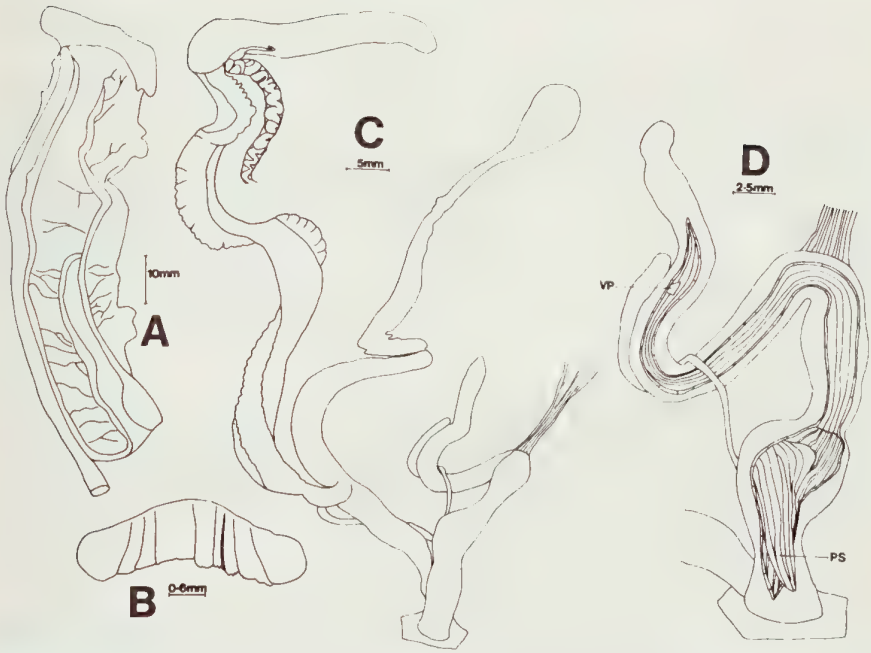

FIGURE 1. *Thersites richmondiana* (Reeve), Binna Burra, Lamington National Park, Queensland. (QM). A-pallial complex, B-jaw, C-reproductive system and D-penial complex. (PS penial papilla, VP vas papilla.)

is quite distinct from that of *Thersites* (Bishop, in press). For this reason Pilsbry's account is somewhat confused and Burch's (1976: 146) reference to Pilsbry's fairly careful study is not entirely justified.

Fulton (1904) realised that Pilsbry was mistaken about the affinities of *H. mitchellae* and placed the species in the section *Thersites*. Iredale (1933, 1937-8) was dissatisfied with Pilsbry's treatment and felt that many more family and generic units were represented within the genus *Thersites* than had been allowed. The cursory nature of the descriptions with which Iredale introduced his new taxa are legendary, and this has led to the suspicion that many may be nomina nuda (Solem, 1964), though this has been denied (McMichael, 1964). No further anatomical evidence being available, Zilch (1959-60) followed Pilsbry's treatment of the group, with some changes in rank.

Shell: The shell of *Thersites* is large and solid, at least 15 mm in height and 25 mm in width. The shape is variable according to species. The umbilicus is open in juvenile specimens but closed in the adult. There are 5½ – 6 whorls and a brown periostracum with granular sculpture (Fig. 4C–E). The shell is marked with chestnut and yellow-brown bands, light on the keel and dark below the suture, above the keel and around the umbilicus. The width of the bands is variable so that shells may appear yellow with brown lines or brown with yellow lines. A common form of *T. richmondiana* is entirely dark brown. The peristome is thick, expanded, reflexed and glossy dark brown and may be sinuous and somewhat toothed.

Anatomy: External appearance fo the animal is not distinguishable from *Sphaerospira* (Bishop in press) except that the dorsal grooves on the neck are somewhat more prominent with a light coloured line between them. There is no keel on the back, and the collar has the usual left and right body lobes.

The pallial complex is sigmurethrous with the gut ureter closed all the way to the collar (Fig. 1A). Delhaye & Bouillon (1972) were wrong to attribute an open secondary ureter to *Thersites* as "*T. meridionalis*" (Brazier) is not a member of the genus. The kidney is very long and narrow, being ten times as long as broad, half the length of the lung roof and three and a half times the length of the pericardium. The apical angle of the lung does not extend beyond the kidney.

The free retractor muscles have the same pattern as *S. fraseri*, the buccal, and left and right compound retractors all being separately inserted at the columella. The right ocular retractor passes between the penis and the vagina.

The jaw is strong and ribbed (Fig 1B, 2, 3A), though the width of the ribs is somewhat irregular. The radula teeth (Fig. 2, 4A–B) are unicuspid except for the marginals which have a long bicuspid inner tooth and a small ectocone which may be further divided according to Pilsbry (1895: 126). The salivary glands are fused over the oesophagus. The crop and stomach present the same internal appearance as in *S. fraseri*: there is a short crop fold running to the entrance of the duct of the anterior part of the digestive gland, a longer crop fold arises sooner and runs to the posterior opening; there is a small triangular accessory fold and the usual typhlosoles are present.

The ganglia of the visceral chain are concentrated and the left parietal ganglion is fused with the visceral ganglion.

The ovotestis is embedded in the digestive gland and consists of five coalescent lobes with numerous ovoid alveoli. The hermaphrodite duct is much convoluted along the middle part of its length. It enters the seminal receptacle-fertilisation pocket complex at the posterior so there is no projecting talon (Fig. 4F). The albumen gland and spermoviduct are like those of *S. fraseri*. The bursa copulatrix is attached to the spermoviduct with connective tissue. The bursa duct is very long with a curious bend about one third to one half of the way from the oviduct (Fig. 1C, 2, 3B). The vagina is bound to the adjacent body wall with tough fibres. The penial complex is enclosed in a thin sheath and has a flagellum with a pointed tip. The proximal part of the epiphallus before the point of insertion of the retractor muscle is indistinguishable internally from the distal part. Flagellum, epiphallus and penis are all lined with fairly even longitudinal corrugations. The penis contains a large imperforate conical papilla which has a longitudinally grooved surface (Fig. 1D, 3C).

Functioning of the penis was studied in an animal of *T. richmondiana* narcotised by injection of nembutal and dissected under saline. A swollen brown coloured atrial disc appears. The penis is everted and the distal part of epiphallus is extruded within it until the retractor muscle reaches the body wall. The basal part of the extruded penis is soft and flexible; towards the orifice it is bulging and corrugated. The papilla forms an extension of the penis with the orifice at its base and a deep groove runs up from the orifice towards the tip of the papilla (Fig. 5). A copulating pair has not been examined and it is not known if spermatophores are exchanged. The length of the vagina is such that the orifice of the extruded penis cannot be brought as far as the opening of the oviduct. The groove in the papilla probably acts to direct sexual products to the base of the bursa duct. The length of the intromittent organ is such that this is possible and the swollen upper region of the penis may help to hold the penis within the vagina.

KEY TO THE SPECIES OF *THERSITES*

1. a. Adult shell almost as high as wide (ratio $>$ 0.8:1) ..... *mitchellae* (Cox)
   b. Adult shell considerably less high than wide (ratio $<$ 0.7:1) 2
2. a. Flagellum short (¼ the length of the proximal part of the epiphallus) and hooked (Fig. 3C) ..... *novaehollandiae* (Gray)
   b. Flagellum longer (½ the length of the proximal part of the epiphallus) and straight (Fig. 1D) ..... *richmondiana* (Reeve)

THERSITES MITCHELLAE (COX)

FIG. 2; 4C; 8–10

Helix mitchellae Cox, 1864 : 19.

Type locality: Clarence River.

Location of type: not traced in the Australian Museum (AM).

Synonym: *Annakelea peragrans* Iredale. 1937: 37, pl.3, Fig. 22. Type locality: Bangalow, Byron

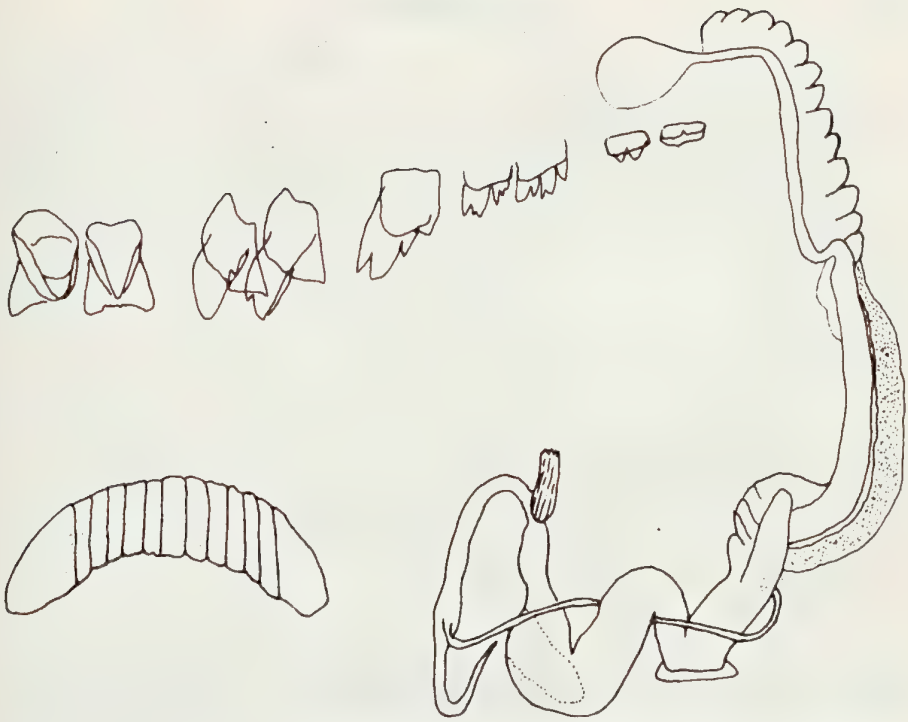

FIGURE 2. *Thersites mitchellae* (Cox). Radula teeth, jaw and distal genitalia. (After Pilsbry).

Bay. Location of type: AM C100663. Iredale considered *H. mitchellae* angulate at the periphery, whereas his new species was not. Examination of a series of specimens shows that there is a transition between the two states.

Diagnosis: The shell is large (40 mm high) and elevated (height:width 0.9:1); angulation of the periphery is weak or absent. Shell sculpture consists of closely packed granules (Fig. 4C). The flagellum is about as long as the proximal part of the epiphallus (judging by Pilsbry's figure, Fig. 2).

Distribution: (Fig. 6). New South Wales 28° 30'S 153° 30'E Ballina (AM), Bangalow (AM), Broken Head (AM), Byron Bay (AM), Emmigrant Ck. (AM), Tweed River (QM); "Richmond River" (AM); "Clarence River" (AM).

This species has not been collected for over fifty years and the only preserved animal in existence is probably that examined by Pilsbry and housed in the Academy of Natural Sciences, Philadelphia. The species occurred in the southern part of the range of *T. richmondiana* but had a more lowland and coastal distribution. The rain-forests where the species probably occurred have largely been destroyed, but a search for living colonies would be worth while.

THERSITES NOVAEHOLLANDIAE (GRAY)

FIG. 3; 4B, D; 11–13

Carocolla Novae Hollandiae Gray, 1834: 67.

Type locality: in Nova Hollandia, 200 millia passuum ab Ostio Fluvii Macquarrie. Subsequently designated as Scone, New South Wales by Iredale (1937).

Location of type: not traced in the British Museum (BM).

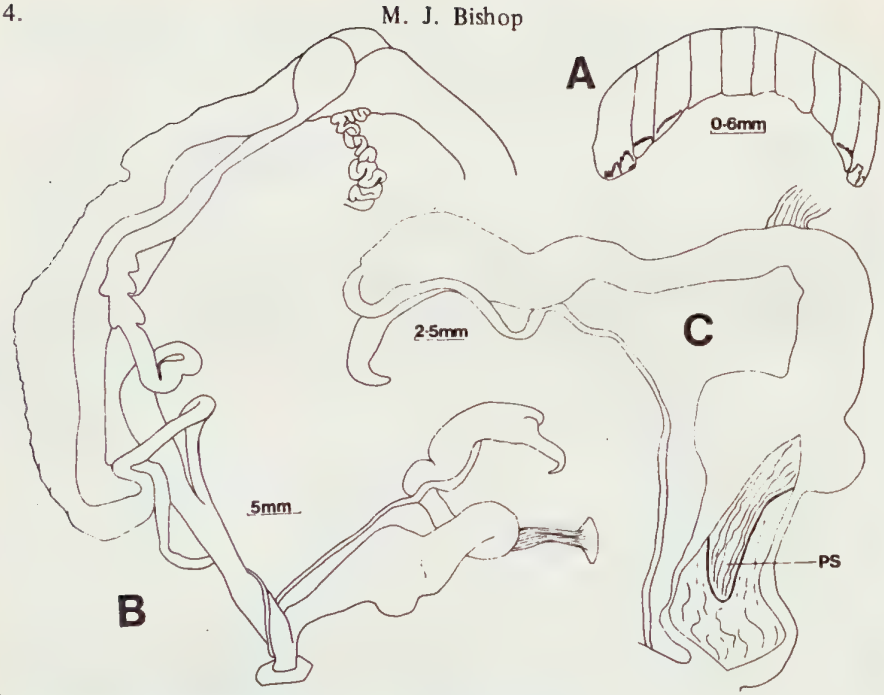

FIGURE 3. *Thersites novaehollandiae* (Gray), Dorrigo State Park, New South Wales (AM). A-jaw, B-reproductive system, C-penial complex. (PS penial stimulator.)

Synonyms: *Helix Dupuyana* Pfeiffer, 1851: pl. 124, fig. 15-16. Type locality: Ostkuste von Neuholland. Location of type: BM 197732 (2 syntypes). In his description Pfeiffer made no reference to the *C. novaehollandiae* of Gray.

Diagnosis: The shell is usually small (20 mm high) and depressed (height:width 0.6:1) with an angulate periphery. Shell sculpture consists of scattered granules with minute dots on the periostracum (Fig. 4C). The flagellum is only about one quarter the length of the distal part of the distal part of the epiphallus and is distinctly hooked (Fig. 3C).

Animal: "Dark grey to black on dorsal surface, speckled with cream spots; more or less distinct, discontinuous thin creamy white line along the centre of the back; tentacles very dark; sole grey, with orange margins; mantle border orange." (D.F. McMichael, unpublished notes).

Distribution: (Fig. 6). New South Wales 29° 30'S 152° 00'E 33 miles east of Glen Innes (AM); 30° 00'S 152° 00'E Marengo (AM); 30° 00'S 152° 30'E Bellingen R. (QM), Dorrigo State Park (AM); 30° 00'S 153° 00'E Mt. Coryah (AM); 30° 30'S 151° 30'E New England National Park (N.P.) (AM); 30° 30'S 152° 00'E Melrose (AM), Styx R. (AM); 30° 30'S 152° 30'E Nambucca R. (QM); 31° 00'S 152° 00'E Mt. Boss (AM); 31° 00'S 152° 30'E Yessabah Cave (AM); 31° 30'S 151° 30'E Barrington Tops (AM); 31° 30'S 152° 00'E Wingham (AM); 32° 00'S 150° 30'E Scone (AM); 32° 00'S 151° 00'E Mt. Royal State Forest; 32° 00'S 151° 30'E Gloucester (AM), Upper Allyn R. (AM); 32° 00'S 152° 00'E Bulahdelah (AM), Myall Lake (AM), Wallis Lake (AM); 32° 00'S 152° 30'E Charlotte Head (AM); 32° 30'S 151° 00'E Bulga (AM); 32° 30'S 151° 30'E Ash Is. (AM); 32° 30'S 152° 00'E Port Stephens (AM).

Habitat: The species lives in rain-forest or wet sclerophyll forest.

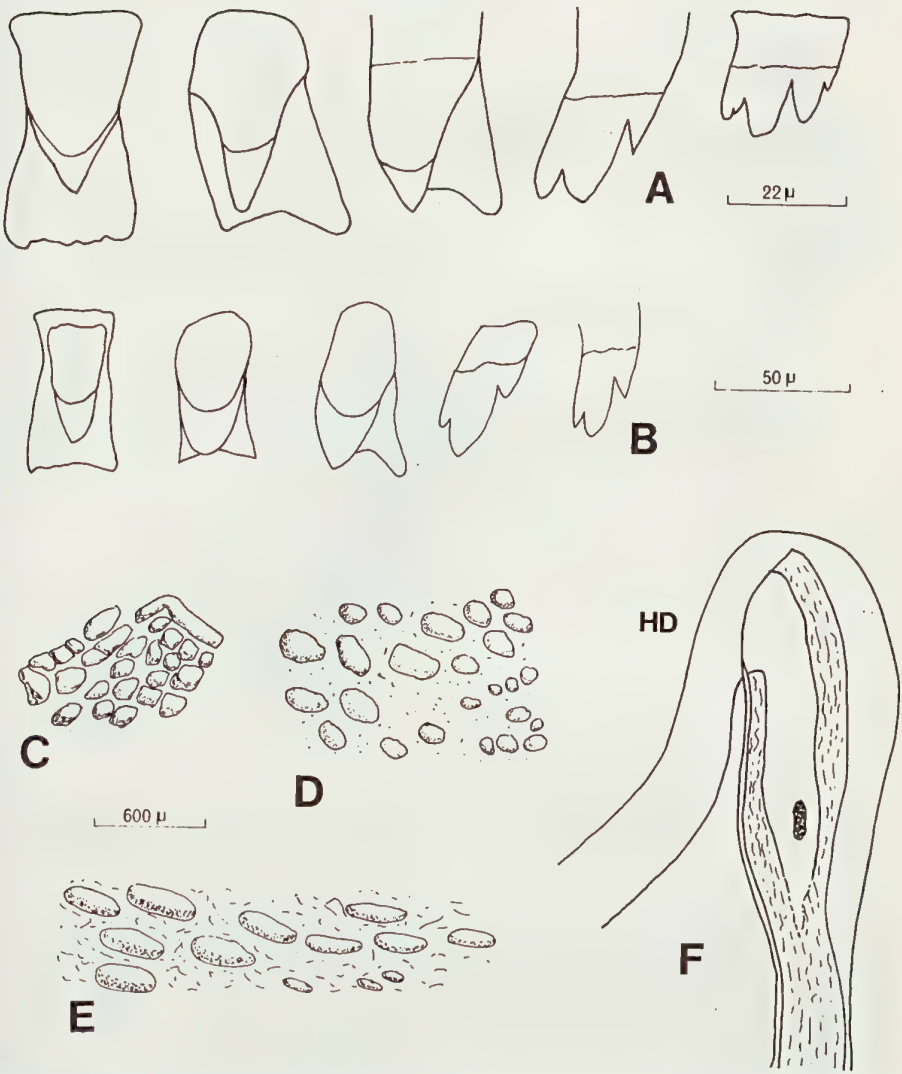

FIGURE 4. *Thersites richmondiana* (Reeve), Lamington National Park, Queensland. (QM). A-radula teeth, E-shell sculpture, F-carrefour region. *T. novaehollandiae* (Gray), New England N.P. (AM). B-radula teeth, D-shell sculpture. *T. mitchellae* (Cox), Tweed River (QM). C-shell sculpture. (HD hermaphrodite duct.)

THERSITES RICHMONDIANA (REEVE)

FIG. 1; 4A, E-F; 5; 14-16

Helix richmondiana Reeve 1852; pl. 70, sp. 365 .

Type locality: Australia. Restricted to Richmond River by Pfeiffer (1853).

Location of type: not traced in the BM.

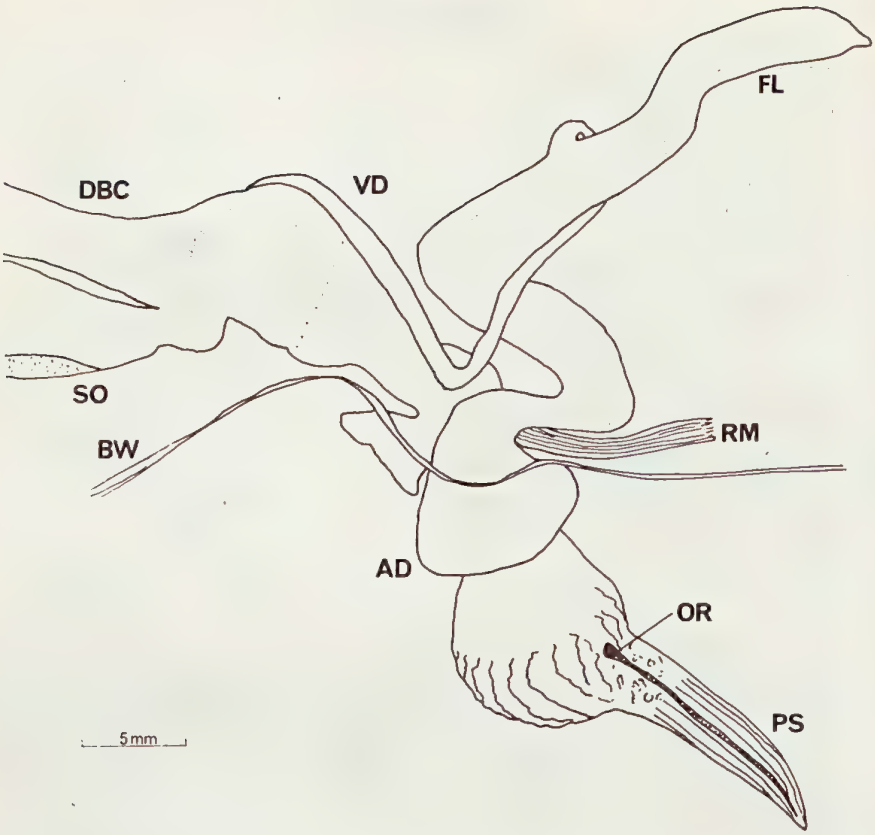

FIGURE 5. *Thersites richmondiana* (Reeve), Lamington National Park, Queensland. (QM). Extruded penis. (AD-atrial disc, BW-body wall, DBC-bursa duct, FL-flagellum, OR-orifice, PS-penial papilla, RM-retractor muscle, SO-spermoviduct, VD-vas deferens.)

Synonyms: *Annakelea tympanum* Iredale, 1937: 38, pl.3, Fig. 25. Type locality: Mt. Tambourine, South Queensland. Location of type: AM C100667. Iredale considered this "a giant relative of *novaehollandiae*" but gave no reason for such an opinion.

Thersites darlingtoni Clench & Archer, 1938: 20, pl.1, Fig. 2. Type locality: MacPherson Range, Queensland National Park, 60 miles S. of Brisbane, Queensland. Location of type: Museum of Comparative Zoology, Harvard (MCZH) 99054. Clench and Archer stated "As compared with *T. richmondiana*, our species has a definately less sharp keel." This is a variable feature as can be determined from examination of a large series of shells. Iredale (1938: 123) considered it a synonym of *A. tympanum*.

Diagnosis. The shell is large (30 mm high) and depressed (height:width 0.7:1) with an angulate periphery and often with a marked keel. Shell sculpture consists of scattered granules with fine periostracal wrinkles (Fig. 4E). Shell colour is often dark brown. The straight flagellum is about half the length of the distal part of the epiphallus.

Shell: The trochiform, acutely keeled shell of *T. richmondiana* has long aroused interest. Similarly keeled, though more depressed shells have been produced by *Caracolus* (Camaenidae, Greater

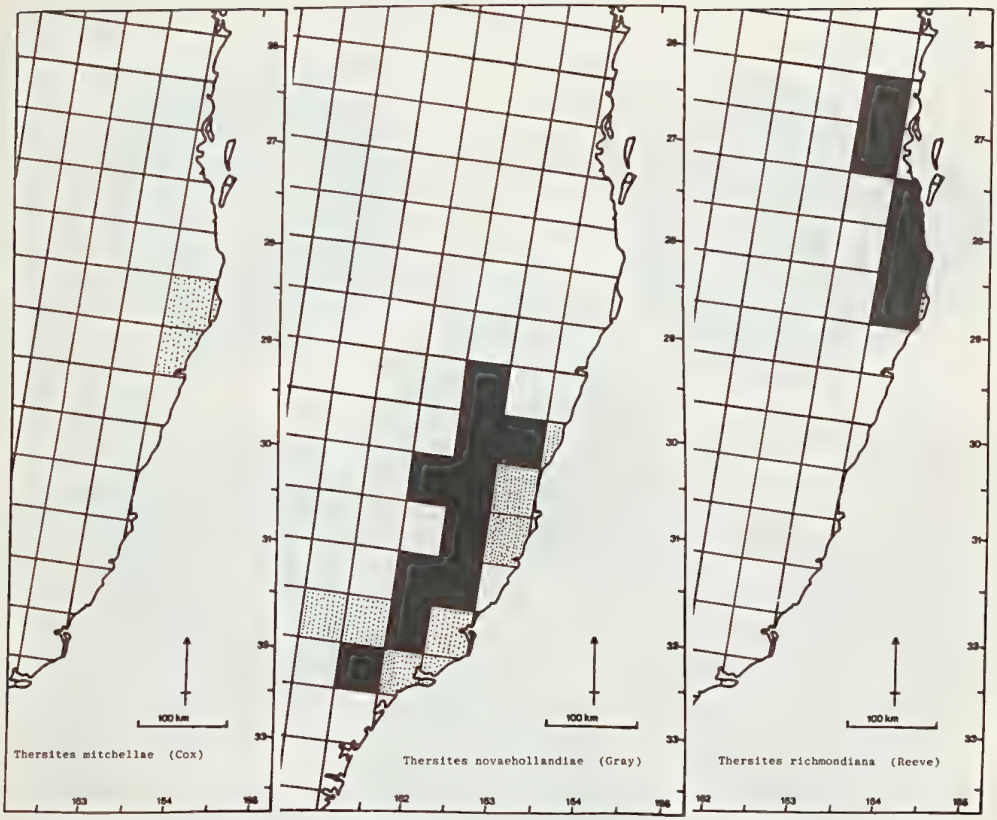

FIGURE 6. Distribution of *Thersites* according to half degree squares of latitude and longitude. Black — records based on dissected material, stipple — records based on shells only.

Antilles), *Pyrochilus* (Bradybaenidae, Moluccas) and *Ampelita* (Acavidae, Madagascar) and may be of adaptive value for a sub-arboreal way of life in tropical or sub-tropical forest.

The shell colour of *T. richmondiana* may be similar to that of the other two species of *Thersites*, and Pilsbry (1890: 91) called this forma *decolorata*. The usual form is dark brown, though there is an entirely albino shell from Nashaw in the Australian Museum.

Animal: The skin pigment is grey with yellow granules. The dorsal grooves on the neck are not deep but are clearly defined by a cream coloured band running between them from the ocular tentacles three quarters of the way back towards the collar.

Distribution: (Fig. 6). Queensland: 26° 30'S 152° 30'E Conondale (QM); 27° 00'S 152° 30'E Mt. Glorious (QM); 27° 30'S 153° 00'E Mt. Tamborine (QM); 28° 00'S 153° 00'E Lamington N.P. (QM), Natural Bridge N.P. (QM), Warrie N.P. (QM); New South Wales 28° 00'S 153° 00'E Mt. Warning (QM); 28° 30'S 153° 00'E Booyong (AM), Dunoon (AM), Nashaw (AM), Whian Whian (AM); 28° 30'S 153° 30'E Mullumbimby (AM), Wollongbar (AM).

Habitat: Rain-forest or wet sclerophyll forest up to 900 m. The animal lives under the bark of trees or under logs on the ground and is entirely nocturnal. It will sometimes feed on leaf litter on the ground but is usually found on the lower parts of trees (up to 5 m) feeding on fungi.

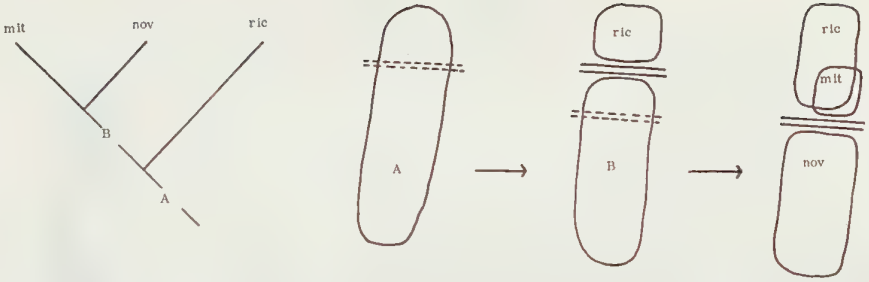

FIGURE 7. An hypothesis of speciation of *Thersites*, mit = *T. mitchellae* (Cox), nov = *T. novaehollandiae* (Gray), ric = *T. richmondiana* (Reeve).

SHELL SIZE AND SHAPE

Sufficient specimens of only one population of each of the three species of *Thersites* were available for statistical study. Measurements of shell height and width were made on mature unbroken shells and recorded in millimetres. The homogeneity of the sample of *T. mitchellae* is suspect as it consisted of shells in the Australian Museum labelled "Bryon Bay" which may have come from a number of separate populations. The shells of *T. novaehollandiae* were collected by S.W. Jackson at Billey's Scrub, Dorrigo in 1900 and the shells of *T. richmondiana* by the author at Binna Burra, Lamington N.P. in 1976 and both represent samples from single biological populations.

Mean values for shell size are presented in Table 1, and the difference between mean height or width of each sample is highly significant (Student's t, one sided test, $P < 0.01$). Shell height constituted the better characterisation of each sample with no overlap in the range of values. These measurements cannot be taken as characteristic of each species and further populations must be studied. A small shell of *T. novaehollandiae* from Mt. Kaputar was only 14.6 mm high and 24.8 mm wide and could not have been drawn from the Dorrigo population ($P < 0.01$). A large shell in the Australian Museum labelled "Dorrigo" measured 28.7 mm high and 40.5 mm wide and could not have been drawn from the Billey's Ck. population ($P < 0.005$) but agrees with the Lamington population of *T. richmondiana* ($P > 0.15$). Care is clearly necessary in using size alone as a specific criterion within the genus.

The way in which height and width vary together gives a measure of the shape of the shells of *Thersites*. The ratio of mean height to mean width of the sample of *T. mitchellae* (0.94) seems distinct from the values for the other two samples but no precise meaning can be given to these figures as height and width are not independent. Highly significant linear regression lines relate height and width (Table 2). As the regression of width on height approaches that of height on width the coefficient b_{WH} approaches $1/b_{HW}$. Only in the case of *T. richmondiana* are these values reasonably close. Comparison of the values of b_{WH} for the three samples showed that the differences were not significant (Student's t, one sided test, $P > 0.15$). The large covariances of height and width in samples of *Thersites* mean that shell shape is not a very reliable criterion for species recognition.

FIGURES 8—16

8-10 *Thersites mitchellae* (Cox). Broken Head, Byron Bay, New South Wales. AM C105563 Jackson leg.

11-13 *T. novaehollandiae* (Gray). Marengo State Forest, Dorrigo, New South Wales. AM C102866 Greer leg.

14-16 *T. richmondiana* (Reeve). Wollongbar, Richmond River district, New South Wales. AM C105562 Helms leg.

All natural size.

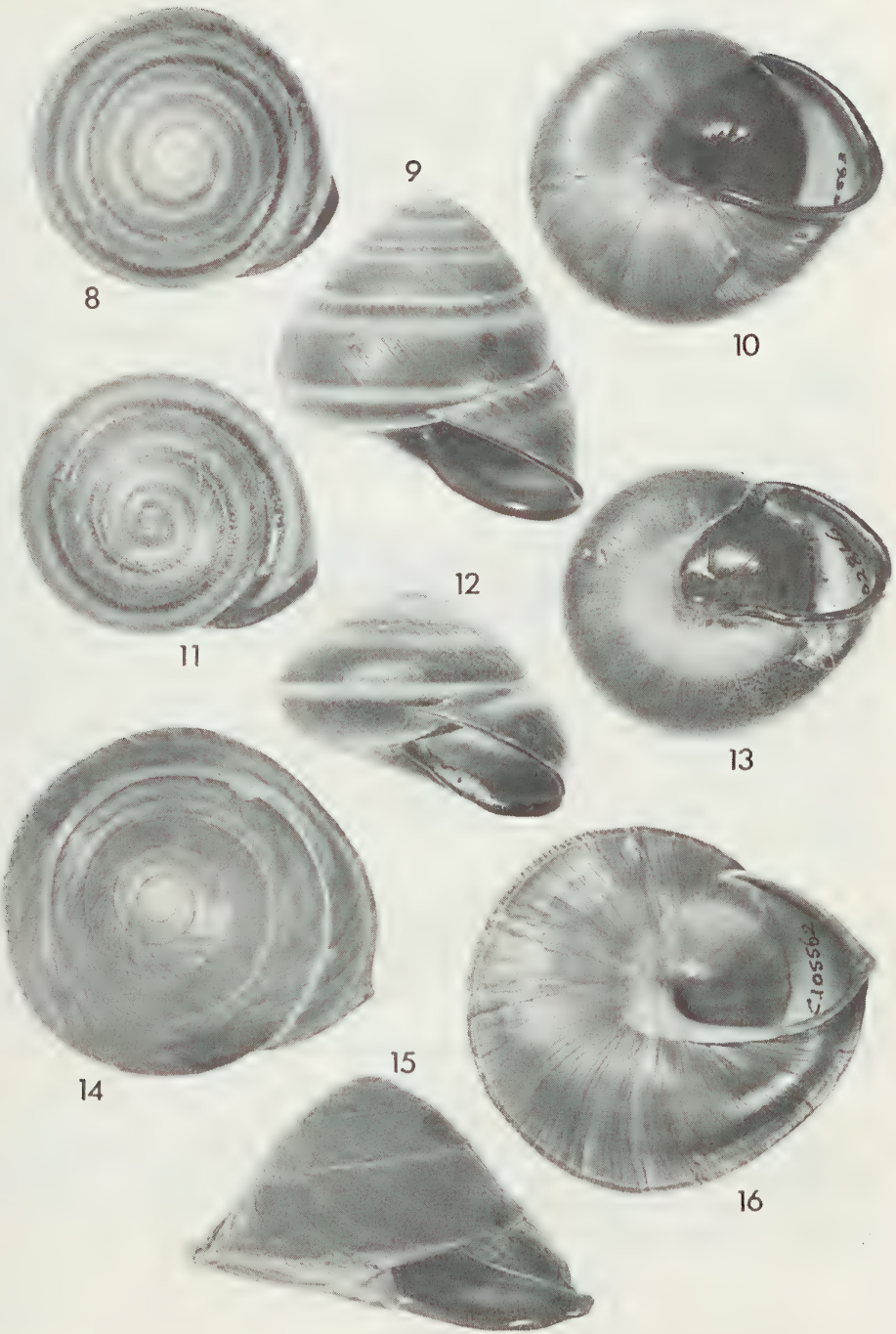
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Table 1. Estimates of size (mm) of the shell of *Thersites*, 16 specimens in each sample.

	Height			Width		
	Mean	Standard error	Range	Mean	Standard error	Range
T. mitchellae Byron Bay (AM)	40.6	0.89	35.5 - 44.8	42.8	0.83	39.5 - 46.6
T. novaehollandiae Dorrigo (AM)	21.0	0.55	17.1 - 25.0	33.8	0.50	30.9 - 38.7
T. richmondiana Lamington (QM)	31.7	0.42	28.9 - 34.7	45.2	0.54	41.3 - 47.8

Table 2. Estimates of shape of *Thersites* in terms of height (H) and width (W)

	Ratio mean H:W	Correlation H with W	Regression coefficients a_W	a_H	b_{WH}	$1/b_{HW}$	Significance of regression F	P
T. mitchellae Byron Bay (AM)	0.94	0.63	18.8	11.7	0.59	1.69	9.3	0.009
T. novaehollandiae Dorrigo (AM)	0.62	0.75	19.4	-6.7	0.68	1.45	15.7	0.001
T. richmondiana Lamington (QM)	0.70	0.73	15.4	6.3	0.94	1.06	18.0	0.001

SPECIATION OF *THERSITES*

If we assume that evolutionary trends within the genus have been in the direction of producing a more depressed, keeled shell and for shortening of the relative length of the flagellum, then *T. mitchellae* has diverged least from a common antecedent (Fig. 7, A). An early vicariant event was the separation of *T. richmondiana* from antecedents to *T. mitchellae* and *T. novaehollandiae* (B). Selection by predation could have led to the predominance of the dark morph of *T. richmondiana*. A second event was the separation of *T. novaehollandiae* to the south and *T. mitchellae* to the north of the Clarence River. This hypothesis implies that the production of depressed shells occurred on two separate occasions, which is insufficiently supported by the morphological evidence. It is favoured because it seems more in accord with the present distribution of the species. A serological study might clarify the situation. Barriers responsible for these events are no longer in evidence and it will be of future interest to discover if such patterns are exhibited by other groups.

RELATIONSHIPS TO OTHER GENERA

Until the details of the anatomy of other camaenid genera, both in eastern Australia and in New Guinea, are made known, it is rather unprofitable to speculate about the relationships of the genus. *Thersites* posseses a number of features which are possibly unique derivations within the taxa of interest: the particular kind of granular sculpture, the dorsal coloured line on the neck, the bend in the bursa duct and the large imperforate conical papilla in the penis. Certainly these features are not possessed by *Hadra, Sphaerospira,* or *Meridolum* which seem more closely related to each other than they do to *Thersites*.

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